Administrative Report

Evaluate Elk Population Control and Support Adaptive Management at Wind Cave National Park

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Abstract

Since 2010, when the National Park Service (NPS) replaced a 6.65-km section of 1.2-m-tall woven-wire fencing along the southwestern boundary, Wind Cave National Park (WICA) has been fully enclosed by a 2.4-m-tall woven-wire fence. To enter or leave the park, elk (*Cervus elaphus*) must negotiate either the fence, cattle guards on roadways, or 7.3-m-wide drop down gates. The NPS proposed to open gates to allow egress and close gates during summer and fall to prevent elk from returning, thereby increasing hunter harvest and causing a gradual decline in population. We used pre-treatment and post-treatment estimates of distribution and vital rates, obtained from elk marked with global positioning system collars, to evaluate effects of the fence renovation on voluntary movements and mortality of elk captured within WICA during winter. During 2005–14, female elk at WICA comprised distinct eastern and western subsets. Elk residing in eastern WICA were essentially confined to the park, whereas elk distribution in western WICA was continuous with elk distribution on adjacent public and private lands. However, the proportion of marked western elk with summer centers of activity outside the park declined from 32% during 2005–09 to 14% during 2011–14. This decline was accompanied by a 32–78% reduction in voluntary use of lands outside the park during January–August. Although the renovated fence and gate system discouraged egress, it did not effectively prevent elk from returning to the park. Consequently, hunting mortality declined from 0.052 (SE = 0.016) during 2005–09 to 0.024 (SE = 0.012) during 2011–14. Effects of reduced mortality from hunting were masked by a coincidental increase in mortality from chronic wasting disease, from ≈ 0.034 (SE = 0.012) to ≈ 0.094 (SE = 0.022). Annual mortality thus increased from 0.132 (SE = 0.024) to 0.187 (SE = 0.030) and projected population growth declined from $\hat{\lambda} = 0.976$ (SE = 0.018) to $\hat{\lambda} = 0.936$ (SE = 0.028). Without knowledge of distribution and cause-specific mortality, changes in population would have created an illusion of success. Our results emphasize inherent risk of interpreting population trend without knowledge of population processes that are directly affected by wildlife management practices, land use, disease, and environmental variation.

Elk were extirpated from the southern Black Hills during the late 19th century. The herd currently occupying Wind Cave National Park (WICA) descended from 21 animals reintroduced from Jackson Hole, Wyoming in 1914 and 30 reintroduced from Yellowstone National Park in 1916.

Prior to 1940, elk numbers at WICA were regulated by sales of surplus elk (Lovaas 1973, National Park Service 1994) and probably also by emigration and poaching. Effects of the latter influences probably declined during the 1940s and 1950s as a result of more effective law enforcement, construction of a park boundary fence, and expansion of the park from 4742 to 11,355 ha. Efforts to herd and bait elk northward, into Custer State Park, were unsuccessful, and by the winter of 1953, elk numbers had increased to 1000–1200 elk. Population control began in earnest during the winter of 1953–1954. During 1953–1957, > 1000 elk were removed from WICA by shooting (Lovaas 1973), reducing the population to approximately 100 animals.

By 1969, elk numbers had increased again to approximately 800 and, in 1970, the National Park Service (NPS) began transferring live elk to tribal, federal, and state agencies. In 1980, live capture and translocation were formally adopted as the preferred alternative for elk population management. During 1969–1994, approximately 2100 elk were removed from the park to achieve and maintain a desired population size of 300–400 head and prevent degradation of park vegetation (Lovaas 1973; National Park Service 1980, 1994).

Translocations of elk from WICA were suspended in 1997, when the first documented case of chronic wasting disease (CWD) in South Dakota was observed in a captive elk herd on adjacent private land. Although state officials ordered the captive herd destroyed to prevent the disease from spreading, an infected elk was discovered at WICA in 2002. The NPS subsequently terminated shipments of potentially infected ungulates from parks (R. Jones, National Park Service 2002, written communication). By 2004, approximately 800 elk occupied WICA for a density of 7.0 elk/km^2, 12–15 times greater than in hunting units surrounding the park and twice the park management objective. The NPS responded by initiating development of an Environmental Impact Statement and Elk Management Plan for Wind Cave National Park [EMP] (National Park Service 2009).

In 2005, we began providing scientific support for development of the EMP by using global positioning system (GPS) telemetry collars to document the movements, distribution, and survival of elk at WICA. In contrast with prior history, we found a stable population ($\lambda = 1.0$) limited by relatively high mortality rates and low recruitment rates. Principal causes of mortality included hunting west of the park, cougar (*Puma concolor*) predation, and chronic wasting disease (Sargeant et al. 2011).

Population stability afforded an opportunity to possibly "tip the balance" of mortality and natality and attempt a population reduction by facilitating hunter harvest outside the park. The NPS replaced 1.2-m 3-strand wire fence along the southwest boundary with 2.4-m woven wire, and installed a series of 7.3-m-wide drop-down gates that could be left open during spring and summer to permit egress and closed in fall to discourage reentry. Thus, the NPS hoped to capitalize on natural movements to accomplish a redistribution of elk, increase adult mortality, and reduce elk numbers from > 800 to < 475 (National Park Service 2009).

The EMP referenced monitoring of elk numbers and movements as key to evaluating effects of the fence on population. However, effects on distribution and mortality were prerequisites for an effect on population. Further, effects of the fence on distribution and mortality were more readily estimable,

less likely to be conflated with effects of other influences, and could more directly inform adaptation of management practices if population objectives were not achieved. For example, failure to achieve a population reduction could result from improved recruitment of calves, from reduced egress of elk from the park, or from insufficient hunter harvest of elk leaving the park. With these issues in mind, we continued monitoring distribution, movements, and survival of marked elk during 2011–14. Herein, we compare and contrast areas used by elk, rates of egress, residency times, rates and causes of mortality, and population growth rates during 2005–09 and 2011–14, before and after implementation of the EMP and modification of the park boundary fence.

STUDY AREA

During our study, elk range within WICA encompassed 11,451 ha of rolling mixed-grass prairie and ponderosa pine (*Pinus ponderosa*) forest along the southeastern margin of the Black Hills in South Dakota (Fig. 1). Size of the park increased by 2248 ha in 2011 with purchase of an adjacent ranch known as the Casey addition; however, the pre-existing park boundary fence effectively prevented access by elk. Common grasses included little bluestem (*Schizachyrium scoparium*), needle-and-thread (*Hesperostipa comata*), western wheatgrass (*Pascopyrum smithii*), and blue grama (*Bouteloua gracilis*). The climate was semiarid, with mild winters and warm summers; during our study, average temperatures ranged from -2 C in January to 24 C in July and precipitation totaled 35 cm in 2006 to 65 cm in 2014 (WICA, unpublished data). Prominent landmarks are depicted in Fig. 2.

The first cases of CWD in South Dakota were documented in 1997 in a captive elk herd held on the Casey addition. The disease was not known to occur in free-ranging deer until 2001 or in elk until 2002 (Gigliotti
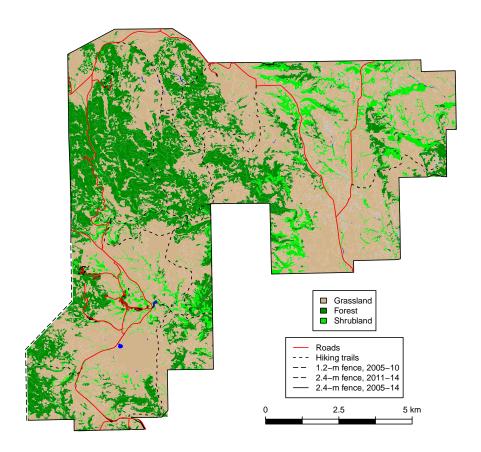
(2004); S. Griffin, South Dakota Game Fish and Parks [SDGFP], oral communication). In 2002, WICA became the only national park outside the core endemic area described by Williams et al. (2002) where CWD was then known to occur.

Potential predators of elk included coyotes (*Canis latrans*) and cougars. Cougars were classified as "threatened" in South Dakota until 2003, just prior to the beginning of our study. Population estimates for the Black Hills of South Dakota (approx. 8,400 km^2), including WICA, increased from 40–50 in 1997 (South Dakota Game, Fish and Parks 2005) to 127–149 in 2003 (Fecske 2003), 164–171 in 2005 (South Dakota Game, Fish and Parks 2005), 220–280 in 2008 (John Kanta, SDGFP, oral communication), and approximately 200–250 in 2010 (South Dakota Game, Fish and Parks 2013). Elk numbers at WICA increased concurrently, from 250-300 in 1995 to approximately 815 in 2005. In addition, the park was occupied by 400-500 bison (*Bison bison*), 200-225 mule deer (*Odocoileus hemionus*), 90–100 pronghorn (*Antilocapra americana*), and approximately 60 white-tailed deer (*O. virginianus*). Black-tailed prairie dog (*Cynomys ludovicianus*) colonies encompassed approximately 1,100 ha of park grassland (approximately 10% of park area; National Park Service 2009).

During 2005–09, WICA was bounded by 53.1 km of 2.4-m-tall woven-wire and 6.4 km of 1.2-m-tall wire bison-proof fence (Fig. 1). Elk traversed the boundary, primarily over the section of low fence, and comingled with the greater Black Hills population (National Park Service 2009). During 2010, the 6.4 km section of 1.2-m fence was replaced with 2.4-m fence and 8 7.2-m-wide drop down jump gates were installed (Fig. 3). The Casey addition was also separated from the remainder of WICA by 2.4-m fencing.

WICA was bordered on the north by Custer State Park, on the west by Black Hills National Forest, and on the east and south by

Figure 1: Vegetation of Wind Cave National Park, South Dakota

Grassland
Forest
Shrubland

Roads
Hiking trails
1.2–m fence, 2005–10
2.4–m fence, 2011–14
2.4–m fence, 2005–14

0   2.5   5 km

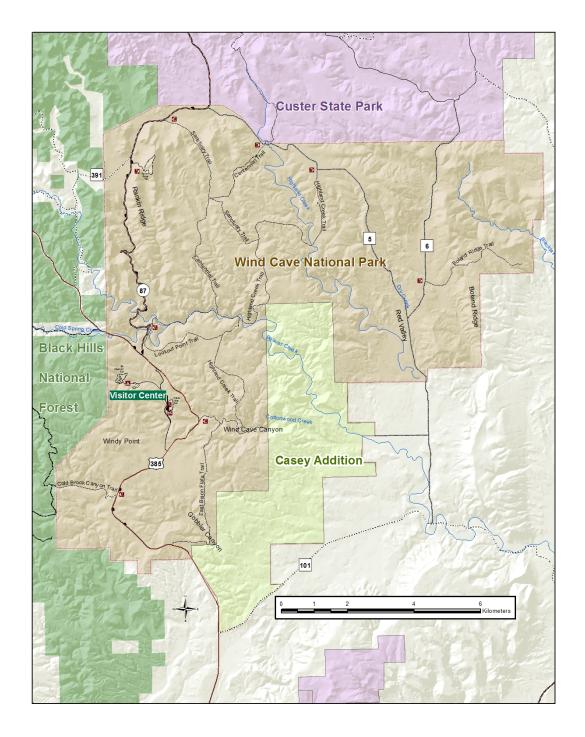Figure 2: Prominent landmarks in and near Wind Cave National Park, South Dakota.

Figure 3: Elk leaving Wind Cave National Park via a drop-down gate installed in 2010. National Park Service photo.

private lands (Fig. 1). Black Hills National Forest was managed for multiple use by the United States Forest Service. Custer State Park was managed for public recreation and wildlife conservation by the SDGFP. Private lands were managed primarily for livestock production, agricultural production, and tourism.

METHODS

Capture and marking

We deployed store-on-board GPS collars (Model G2000, Advanced Telemetry Systems, Isanti, Minnesota, USA) on yearling male and yearling and adult female elk during February of 2005–08 and 2011–13. Sample elk were captured in WICA, with a helicopter and net gun, by Leading Edge Aviation (Clarkston, Washington, USA) in accordance with a park-approved flight safety plan. We collected a blood sample for pregnancy testing (Noyes et al. 1997) by Bio

Tracking (Moscow, Idaho, USA), estimated age-classes (e.g., yearling, adult, old adult) from dentition (Hudson et al. 2002), and installed a uniquely numbered metal tag in one ear (prior to 2008) or in each ear (2008 and later). We retrieved collars and downloaded data when elk died or after 11–36 months, when batteries were exhausted. Ear tags uniquely identified individual elk if they were recaptured, found dead, or killed by a hunter after collars had been retrieved.

If elk exhibited substantial tooth wear characteristic of ages > 8 years, we extracted a vestigial upper canine tooth for determination of age from cementum annuli by Matson's Laboratory (Milltown, Montana, USA). Tissue surrounding the base of the tooth to be extracted was treated with topical cetacaine, then infused with a local anesthetic (4 ml of a 1:1 mixture of lidocaine and bupivacaine) to reduce discomfort during extraction. To reduce post-procedural discomfort, elk were given an oral dose of phenylbutazone paste (4mg/kg), applied to the inside

of the cheek by syringe. We also administered an injection of penicillin (20 ml of procaine + benzethene; approximately 22,000 units/kg). To prevent human consumption of residual antibiotic or phenylbutazone, elk were captured after the annual hunting season and collars were labeled with a warning to discourage consumption. Procedures were reviewed and approved by Institutional Animal Care and Use Committees of the USGS Northern Prairie Wildlife Research Center and NPS.

Because CWD was known to occur in elk at WICA, we took great care to prevent transmission during capture or via GPS collars. When we recovered and refurbished collars, we removed and destroyed belting before soaking the receiver and associated metal container in an aqueous solution of 10% Environ LpH (Steris Corporation, St. Louis, Missouri, USA) for ≥ 1 h. Members of the capture crew wore disposable surgical gloves while handling elk and did not reuse syringes, needles, or gloves. Each year, after completion of capture operations, nets were either destroyed or 1) washed in hot soap and water to remove gross contamination, 2) soaked in 10% solution of Environ LpH for ≥ 1 h, and 3) triple rinsed and air-dried.

Data collection

Collars estimated and recorded locations of marked elk at 5-h (2005) or 7-h (2006–14) intervals throughout the year. Sampling at primary intervals provided 3–4 locations per elk per day and evenly distributed sampling throughout the day and night. For example, if an elk was located one day at 0100, 0800, 1500, and 2200 hours, it was located the next day at 0500, 1200, and 1900 hours and a day later at 0200, 0900, 1600, and 2300 hours. This rotating schedule assured representative sampling and eliminated bias that might otherwise result from temporal activity patterns. In addition, we monitored each marked elk at 15-minute intervals for 24 h

on dates selected to maximize coverage of biologically significant periods, within constraints imposed by battery life.

GPS collars included very high frequency (VHF) transmitters, which operated for 4 days per week. The VHF transmitters included mortality sensors, which were checked weekly so that causes of death could be determined and collars could be recovered if elk died during the course of our study. Whenever possible, we collected a sample of brain tissue for immunohistological CWD testing by the Colorado State University Veterinary Diagnostic Laboratory and assigned elk to 1 of 3 condition classes (Table 1). Proximate causes of death were inferred from physical condition, infection with CWD, harvest reports (hunting), characteristic injuries or caching of carcasses (cougar predation; Shaw et al. 2007), fatal bullet wounds (poaching), entanglement of carcasses in fences (fence), vehicle accident reports and massive blunt trauma (vehicle), and restricted post-marking movements of otherwise healthy elk (excluded from analysis). We used cessation of movement, determined from GPS locations and activity-sensor records stored by collars, to determine dates of death. We terminated survival records for elk at death, when collars failed (indicated by low-battery signals or malfunctioning VHF radio transmitters), or at scheduled dates of collar retrieval.

Data analysis

We plotted and visually inspected GPS locations of elk to identify malfunctioning collars and anomalous records. Collar malfunctions were evident from erratic spatial arrangements of temporally ordered locations. Anomalous records included locations with inadmissible values and locations that were biologically implausible. We excluded malfunctioning collars and anomalous locations from our analysis. When computing home ranges of individual elk, we also excluded

Table 1: External and internal characteristics used to describe physical condition of deceased elk at Wind Cave National Park, 2005–14.

Condition class	External characteristics	Internal characteristics
Poor	Emaciated or shrunken appearance. Angular rump profile, hollow flanks, pelvis, ribs, and vertebrae prominent.	Subcutaneous, omental, and kidney fat absent. Carcass red or raw in appearance. Femur marrow translucent, gelatinous, pink-to-amber.
Fair	Ribs and vertebral crest palpable, but not prominent or visible.	Subcutaneous, omental, and kidney fat present. Femur marrow opaque and firm.
Good	Notably plump, robust appearance. Ribs, pelvis, and vertebral crest padded with fat and flesh.	Omentum netted with ribbons of fat. Kidneys hidden by fat. Femur marrow opaque, white, firm.

locations obtained within 2 weeks of capture or herding of elk with helicopters. We used characteristic polygons with minimum edge lengths of zero to generate individual home ranges depicted in this report (Duckham et al. 2008).
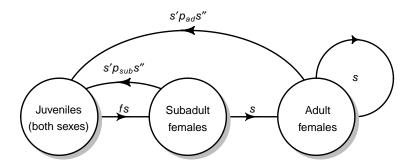
We used spatial medians of locations (Vardi and Zhang 1999, Nordhausen et al. 2012) to represent summer (i.e., Jun–Aug) centers of activity for elk with > 100 summer locations. To depict the intensity and variability of seasonal elk activity, we tallied subsets of locations (e.g., summer locations of elk with summer activity centers in eastern WICA) in 1 ha hexagonal grid cells. We divided the count for each cell by the maximum count for all cells and used values to color-code cells overlaid on maps of the park. When we estimated centers of activity and distributions of elk activity, we excluded locations of elk that were outside the park because they were herded out on 1 March 2013, 8 March 2013, or 12 March 2014. When we estimated proportions of time spent within the park, we excluded elk with fewer than 45 locations for a given month. When plotting distributions of elk activity and computing proportions of time elk spent outside WICA, we excluded

locations obtained after 1 March, 2013, when distributions and movements were first altered by herding elk out of the park. To minimize spurious changes in status resulting from GPS error, we required ≥ 2 successive locations > 100 m from the park boundary fence to classify elk as "in" or "out" of the park. When computing proportions of locations that were outside the park, we excluded wholly resident elk with summer centers of activity in eastern WICA.

We used 24-h sequences of locations obtained at 15-minute intervals with $\geq 95\%$ fix success to identify locations where elk crossed the park boundary fence during 2011–14. Most "crossings" suggested by sequences were results of GPS or map error, such that elk near the fence were occasionally misclassified as "out" of the park or, less frequently, as "in" the park. We plotted and evaluated potential crossings that included 1 location on each side of, and at least 10 m from, the park fence. "Confirmed" crossings were inferred from clear evidence of directed movement from one side of the park fence to the other.

We used a 3-stage matrix projection model (Figure 4) that accurately described the

Figure 4: Model used to project growth of a hypothetical elk population. States reflect ages on 1 September. Parameters represent the proportion of juvenile females (f), subadult and adult pregnancy rates (p_{sub} and p_{ad}), and survival probabilities (s, annual survival; s', survival from 1 September to 1 June; and s'', prenatal-neonatal survival from 1 February to 1 September).

growth of several elk populations (Sargeant and Oehler 2007) to explore implications of survival and pregnancy rates for population growth. To reflect uncertainty resulting from parameter estimation, we used bootstrap estimates of survival, pregnancy rates generated by sampling binomial distributions, and calf:adult female ratios drawn from a normal distribution with mean and standard error estimated from field observations to fit our model 1000 times. For each iteration, we generated an estimate of perinatal survival (from fetus in January to approximately 3 months of age) by adjusting s' in our model until the projected calf:adult female ratio and corresponding sample ratio matched.

We used the R language and environment, v. 3.1.3 (R Foundation for Statistical Computing. 2015. http://www.R-project.org, accessed 20 December 2015) to perform statistical analyses and fit our model. We used the nonparametric cumulative incidence function estimator of Heisey and Patterson (2006) to estimate cause-specific mortality. Our implementation of the estimator, associated documentation, and examples are provided in an R package, *wild1* (Sargeant 2016). R code for estimation of characteristic polygons is available from the authors upon request.
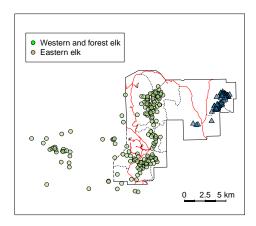
RESULTS

Spatial organization

Throughout the course of our study, female elk at WICA comprised 2 relatively distinct groups, with limited overlap in the north-central portion of the park. Sixty-one elk with summer centers of activity within the park and east of the Highland Creek Trail in northern WICA (hereafter "eastern elk") resided primarily in the area of Boland Ridge, along the eastern boundary, and were largely confined by the park boundary fence. For eastern elk, only 2 of 76 summer centers of activity (2.6%) were outside the park. In contrast, 121 elk with summer centers of activity west of the trail (hereafter "western and forest elk") were distributed continuously from north to south along the western boundary of the park and to the west outside the park (Figure 5). For western elk, 25 of 77 centers of activity (32%) were outside the park during 2005–09 and 14 of 102 (14%) were outside the park during 2011–14.

During summer (Jun–Aug), activity of eastern elk was heavily concentrated on the western side of Boland Ridge, north of the Boland Ridge Trail, in the vicinity of Blacktail Creek (Figure 6), and also in a smaller region west of Red Valley, along the park boundary. During winter (Dec–Feb), the area of most intensive use expanded southward along Boland

Figure 5: Two-hundred-fifty-three centers of summer activity for 181 elk tracked with global positioning system collars at Wind Cave National Park, South Dakota, during 2005–14. Two centers northeast of the park are not shown.

Ridge to the southern boundary. Low intensity use expanded westward into northern areas used intensively by western and forest elk during summer (Figure 6).

Within WICA, summer activity of western and forest elk was broadly distributed from north to south along the western boundary with relatively intensive use in the vicinity of Windy Point, Gobbler Canyon, Wind Cave Canyon, east of Rankin Ridge, and west of Highland Creek (Figure 7). Activity was more concentrated and shifted southward during winter, particularly from south and west of Lookout Point Trail to Cold Brook Canyon Trail (Figure 7).

Movement across park boundaries

Prior to 2010 and renovation of the boundary fence, use of WICA by marked elk was highly variable. We captured winter residents that rarely, if ever, were observed outside the park; migrants with winter ranges inside the park and summer ranges outside; and elk with winter ranges that spanned the park boundary. Because we captured elk only inside the park, elk with winter ranges that spanned the park boundary were underrepresented and elk with winter ranges out-

side WICA were not included in our sample. Accordingly, proportions of locations within WICA during 2005–09 (Figure 8) were useful for description of behaviors and as an index of seasonal variation, but probably overestimated use of the park. This bias was reduced by renovation of the park fence and concomitant reduction of movement across the park boundary (Figure 9). Accordingly, the effect of renovated fencing was likely greater than suggested by Figure 8.
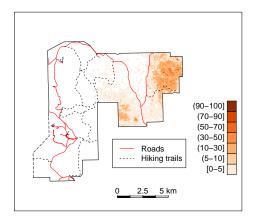
Seasonal use of lands outside the park followed a similar pattern before and after renovation of the fence (Figure 8). Use of surrounding lands increased during December–January, after the elk hunting season; decreased during February–March; increased markedly during April–May; began declining in late June; and was lowest during October and November. However, renovation of the fence dramatically reduced the proportion of locations outside the park during December–August. Moreover, the renovated fence may have slowed, but did not prevent, elk from returning to the park during July–October.

During any given 30-day period prior to renovation of the park fence (Figure 9, top), 25–85% of marked western and forest elk resided within WICA, 0–32% resided outside WICA, and 13-71% made some use of range both within and outside the park. After renovation, the percentage of marked elk residing entirely within the park during any given 30-d period was greater and less variable, ranging from 68 to 92%. This increase resulted primarily from concomitant decreases in intermittent use of park and adjacent lands.

During 2011–14, we obtained 1994 24-h trajectories of locations acquired at nominal 15-minute intervals with > 95% fix success. Review of these candidates revealed just 3 confirmed fence crossings by collared elk (Appendix I).

Thirty-four collared elk were herded out of the park by the NPS during 2013 (28) and

Figure 6: Distributions of 23,249 summer (Jun–Aug) locations of 57 elk (left) and 11,356 winter (Dec–Feb) locations of 59 elk (right) in eastern Wind Cave National Park, South Dakota, 2005–14. Colors indicate relative use (percent of maximum) for 1-ha hexagonal grid cells.
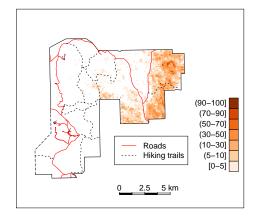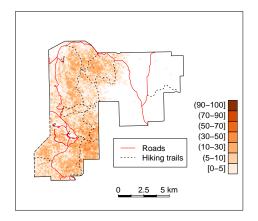

Figure 7: Distributions of 45,147 summer locations of 107 elk (left) and 25,799 winter locations of 115 elk (right) in western Wind Cave National Park, South Dakota, 2015–14. Colors indicate relative use (percent of maximum) for 1-ha hexagonal grid cells.
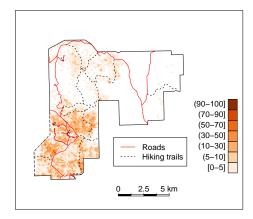
Figure 8: Proportions of time spent within Wind Cave National Park by marked western and forest elk during 90 day moving windows, 2005–09 and 2011–12. Ninety-percent bootstrap confidence limits about the difference between curves do not include zero except where indicated by dashed lines.
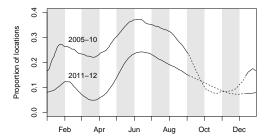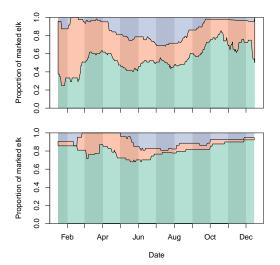

Figure 9: Proportions of marked western and forest elk residing entirely inside (≥ 97.5% of locations within the park, bottom region), partially inside (2.5–97.5% of locations, center region), or entirely outside (≤ 2.5% of locations, top region) Wind Cave National Park during 30-day moving windows, 2005–09 (top figure) and 2011–12 (bottom figure).

2014 (6). Return times and fates are shown in Figure 10. At least 50% (17) successfully negotiated the boundary fence and returned within approximately 4 months (124 days).
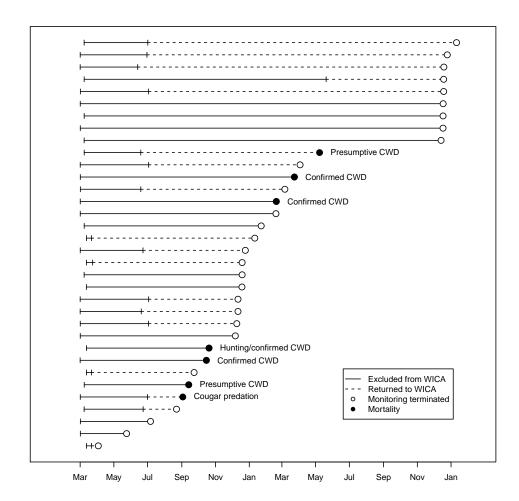
Collared elk that were herded out of the park during 2013 were pushed northward, into Custer State Park, on 1 or 8 March. Thirteen of those elk returned to the park by 3 July 2013 and 1 returned on 20 May of 2014 (Figure 10). Of the 14 that did not return while they were still under observation, 4 died outside the park from confirmed (3) or presumptive (1) CWD. In addition, one elk that returned to the park died subsequently from CWD.

All marked elk that were herded northward remained in the vicinity of WICA: 60% of locations were within 1 km, 90% were within 2 km, 98% were within 3 km of the park. Movement may have been impaired by fences on the east, northeast, and west, as evinced by corresponding locations of fences and discontinuities in the distribution of activity. However, fences apparently did not prevent elk from dispersing to the north if they were so inclined (Appendix II).

Collared elk that were herded out of the park during 2014 were pushed westward, into the Black Hills National Forest, on March 12. Three of these elk were apparently together when they were last located outside the park on March 21, in the vicinity of Custer County Road 391, which traverses the park boundary at 620970 E, 4830851 N, Universal Transverse Mercator (UTM) zone 13. The fourth returned via a similar route on March 23 or 24. One elk remained outside the park until it was killed by a hunter on October 20, 2014, and was also infected with CWD. One elk survived outside the park until collar recovery on December 18, 2014.

Unlike elk that were herded northward, the two elk that remained west of the park probably were not displaced from their own traditional ranges. Both occupied ranges within

Figure 10: Return intervals and fates of elk herded out of Wind Cave National Park (WICA) during March, 2013 and 2014. "CWD" denotes chronic wasting disease.

the park that were previously bounded by 1.2-m woven-wire fence, and both occupied ranges outside the park that were contiguous with their ranges in the park (Appendix III). Moreover, both probably were adults, based on dentition, when the park fence was renovated in 2010.

Mortality

We obtained survival records for 84 subadult male and 215 female elk. Records encompassed 132,183 elk-days of observation and 61 deaths. Mortality rates and numbers of deaths attributed to various causes are shown in Table 2.

In 25 cases, collared elk simply "laid down and died" without evidence of injury. Such elk, when tested for CWD, were invariably infected [Table 2, first row and Sargeant et al. (2011)]. Given the strength of this association, CWD was likely the cause of death for similar, untested cases (Table 2, second row). Annual mortality rates for confirmed and presumptive CWD, combined, were 0.034 (SE = 0.012) during 2005–09 and 0.094 (SE = 0.022) during 2011–14. In addition, approximately one-third of deaths (32%, SE = 10.2%, n = 22 tests) attributed to other proximate causes were associated with CWD infection. If CWD was regarded as the underlying cause for known cases, the mortality rate from CWD reached 0.042 (SE = 0.013) during 2005–09 and 0.125 (SE =0.025) during 2011–14.

Prior to renovation of the park boundary fence in 2010, hunting outside the park was the leading proximate cause of adult mortality, at 5.2% (SE = 0.016) annually, followed by CWD (Table 2). With renovation of the fence and restriction of movements across the park boundary, hunting mortality declined to 2.4% (SE = 0.012) annually. However, this decline was offset by increased mortality from CWD. Accordingly, our point estimate of total mortality increased from 13.2% (SE = 0.024) during 2005–09 to 18.7% (SE

= 0.030) during 2011–14. Rates of mortality from other causes were relatively stable during 2005–14.

Natality

We tested 22 subadult females and 211 adult females for pregnancy. We observed just two instances (p = 9.1%, SE = 6.13%) of subadult pregnancy. Adult pregnancy rates were similar before (p = 78.2%, SE = 4.11%, n = 101) and after (p = 75.5%, SE = 4.10%, n = 110) implementation of the EMP and averaged 76.8% (SE = 2.91%). Calf:cow ratios in late August/early September averaged 0.311 prior to implementation of the EMP, 0.297 after, and 0.305 for the duration of our study.

Population growth

Given average natality, mortality, and calf:adult female ratios from 2005–14, our fitted value for perinatal mortality was 0.510 (SE = 0.050) and our model projected stable to gradually declining elk numbers ($F\hat{\lambda} = 0.976$, SE = 0.018). Substituting our point estimate for total mortality during 2011–14 had a negligible effect on our estimate of perinatal mortality, which increased to 0.513 (SE = 0.053) but increased the rate of decline to $\hat{\lambda} = 0.936$ (SE = 0.028). Taken at face value, our estimates of λ equated to 10-year population reductions of approximately 20% and approximately 50%, respectively. However, they also highlight the sensitivity of long-term projections to slight changes in λ. We conclude principally that vital rates of elk at WICA are consistent with a stable to declining population and are not consistent with an increasing population and accelerating effects on park vegetation or other wildlife.

MANAGEMENT IMPLICATIONS

Reducing and regulating elk numbers wholly via regulation of voluntary movements across park boundaries could have succeeded only by elevating the risk of extra-park hunting mortality for elk park-wide. Such an effect

Table 2: Rates of mortality ($\hat{\theta}$) associated with various contributing causes for subadult and adult female elk at Wind Cave National Park, South Dakota, during 2005–14. Columns "n" represent numbers of deaths for elk that were tested/not tested for infection with chronic wasting disease (CWD). "CWD+" indicates a positive test for infection with CWD, in combination with another proximate cause of death.

	2005–09				2011–14				Change		2005–14, pooled		
	n	$\hat{\theta}$	SE	90% CI	n	$\hat{\theta}$	SE	90% CI	$\Delta\hat{\theta}$	SE	$\hat{\theta}$	SE	90% CI
Confirmed CWD	3/-	0.013	0.008	0.000, 0.026	11/-	0.062	0.018	0.032, 0.091	0.049	0.020	0.034	0.009	0.019, 0.050
Presumptive CWD	0/5	0.021	0.009	0.006, 0.036	0/6	0.033	0.013	0.011, 0.054	0.012	0.016	0.026	0.008	0.013, 0.039
Hunting, CWD+	0/-	0.000	–	–	1/-	0.006	0.006	0.000, 0.015	0.006	0.006	0.003	0.003	0.000, 0.007
Hunting	4/6	0.052	0.016	0.025, 0.079	2/1	0.018	0.010	0.001, 0.035	-0.034	0.024	0.036	0.010	0.019, 0.053
Cougar, CWD+	1/-	0.005	0.005	0.000, 0.012	3/-	0.016	0.009	0.001, 0.032	0.011	0.017	0.010	0.005	0.002, 0.018
Cougar	1/3	0.017	0.008	0.003, 0.030	1/2	0.016	0.009	0.001, 0.031	-0.001	0.018	0.016	0.006	0.006, 0.027
Vehicle	1/0	0.005	0.005	0.000, 0.012	1/1	0.012	0.008	0.000, 0.025	0.007	0.013	0.008	0.005	0.000, 0.016
Other, CWD+	1/-	0.004	0.004	0.000, 0.010	1/-	0.008	0.008	0.000, 0.022	0.004	0.009	0.005	0.003	0.000, 0.010
Other	3/0	0.016	0.010	0.000, 0.032	2/1	0.017	0.010	0.001, 0.033	0.001	0.020	0.016	0.007	0.005, 0.027
Totals	14/14	0.132	0.024	0.092, 0.171	22/11	0.187	0.030	0.139, 0.236	0.055	0.030	0.154	0.018	0.124, 0.184

could not be achieved at WICA for several reasons. First, the elk population comprised discrete eastern and western subsets. The female segment of the eastern subset were effectively confined to the park and were unaffected by renovation of the southwestern boundary fence. Second, the renovated fence and gate system acted primarily to reduce use of lands west of the park, thereby reducing exposure of western elk to risk of hunting mortality. The effect of reduced egress may also have been magnified by a concomitant reduction in the number of state-issued elk hunting licenses for lands west of the park.

Although attempted management of voluntary movements failed to increase use of adjacent lands or increase mortality from hunting, renovation of the park boundary fence coincided with a presumably unrelated increase in mortality from CWD and a concomitant decline in population growth. If we relied on knowledge of elk numbers rather than elk distribution and vital rates, we would have concluded—incorrectly—that renovation of the park fence accomplished management objectives. Whereas population growth embodies collective effects of all influences on vital rates and distribution, focusing on processes targeted by management actions reduces the likelihood of confounding and spurious inference when replication and experimental control are not possible. Further, knowledge of vital rates and distribution can—as in this case—elucidate reasons for outcomes and inform adaptation of management plans.

Elk numbers within WICA were reduced effectively by herding elk northward into Custer State Park and westward into the Black Hills National Forest. However, elk that were herded away from traditional range into Custer State Park remained concentrated along the WICA boundary fence, which was clearly more effective in deterring egress than entry. We suspect philopatry and social relationships had opposite effects on voluntary egress of elk from the park and return of displaced elk to traditional range within the park. Because displaced elk are highly motivated to return, prompt detection and repair of damaged fencing are likely to be essential components of any plan to exclude resident elk from WICA.

Estimation of mortality is predicated on representative sampling, noninformative censoring, and independence of events. Longitudinal studies of CWD in wild elk are unlikely to satisfy these conditions, and ours did not, so management implications warrant careful consideration. At WICA, we selected outwardly healthy elk and did not pursue animals that showed signs of distress; hence we did not capture elk with advanced CWD. Infection with CWD may elevate risk of predation, accidents, or even capture and handling (Krumm et al. 2005, Williams 2005). Removal of animals from those at risk of death from CWD *because they are infected with CWD* exemplifies informative censoring, and we found evidence of such an effect in the relatively high rate of infection among elk that died of other causes. Our estimates of mortality from CWD were therefore conservative (i.e., subject to foreseeable negative bias). However, CWD is an infectious disease, elk are gregarious animals, and we observed broad overlap of individual ranges. Temporal variation in prevalence and mortality may thus be considerably more variable than would be expected for independent events.

In context with typically high survival rates and typically low prevalence of CWD in elk, annual mortality of elk at WICA during 2011–14 and mortality associated with confirmed or presumptive CWD were exceptional and present substantial long-term challenges for elk management. In combination with low pregnancy rates and high perinatal losses, adult mortality rates were not sustainable. Vital rates were indicative of a population decline that may not be alleviated by compensatory responses to falling elk density. In particular, studies in adjacent Custer

State Park have implicated cougar predation as the cause of similar neonatal losses (Chad P. Lehmann, SDGFP, oral communication). Mortality from cougar predation probably is not proportional to population size, hence is likely to increase, rather then decrease, as elk numbers decline. Likewise, reduced density may not alleviate adult mortality from accidents or hunting. Persistent environmental contamination, the gregarious nature of elk, and the long course of disease from infection to mortality are all likely to diminish effects of density on CWD infection; hence, reducing elk densities may not reverse the increase in prevalence that occurred during ca. 2000 to 2015. If survival and fecundity do not increase, the population will continue declining at similar or greater rates after population objectives have been reached.

Regardless of population trend, elk densities at WICA exceed management objectives established by the NPS to protect native vegetation and other wildlife (National Park Service 2009). Moreover, high elk densities combined with year-round occupation of elk range at WICA, which are likely to promote animal-to-animal transmission and environmental contamination, are a plausible explanation for rapidly increasing prevalence and observed high rates of mortality from CWD (Almberg et al. 2011), which were much greater for marked elk than for elk in the greater Black Hills region, where prevalence is reportedly $< 1\%$ (Sargeant et al. 2011).

In the context of this report, our model is primarily a device for understanding the collective implications of various influences on population and for estimating perinatal mortality and population trend. Our estimates of λ should not be used directly for long-term population projection and management planning because discrepancies between model projections and actual population performance compound over time. Further, discrepancies generally arise because models are simplified representations of actual dynamics, parameter estimates are subject to sampling error, and environmental influences (including risks, e.g., of disease or predation) are subject to change. With these limitations acknowledged, our model and parameter estimates nevertheless provide an objective basis for exploring potential management strategies or hypothetical population responses to changing density.
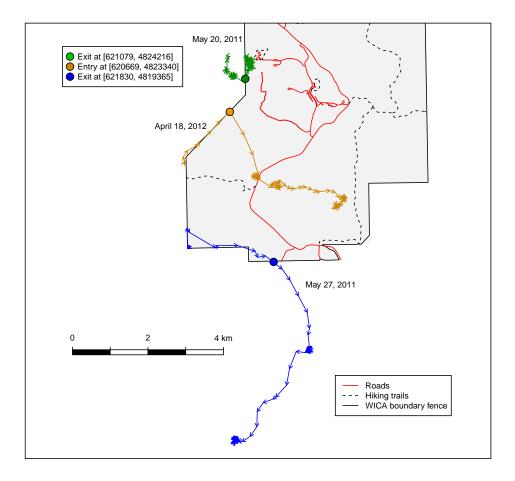
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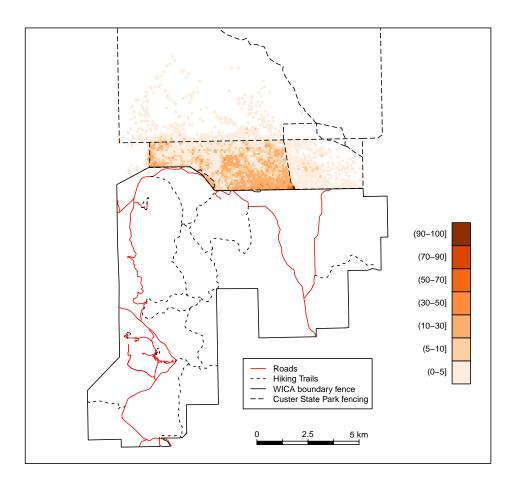
APPENDIX I

Travel routes of 3 elk marked with GPS collars at Wind Cave National Park (WICA), South Dakota, represented by 24-hour series of locations obtained at nominal 15-minute intervals. Filled circles represent estimated locations of park boundary crossings.

APPENDIX II

Distribution of activity in Custer State Park for 28 elk herded out of Wind Cave National Park (WICA) on 1 or 8 March, 2013.

APPENDIX III

GPS locations and characteristic polygon home ranges of 2 female elk herded westward out of Wind Cave National Park on 12 March 2014.